Three new species of *Cystiscus* Stimpson, 1865 (Gastropoda: Cystiscidae) from the Tuamotu Archipelago

Andrew WAKEFIELD
14 Forest Side, Buckhurst Hill, Essex, IG9 5SL, U.K.

Tony McCLEERY
The Moat House, Fort Road, St Peter Port, Guernsey, GY1 1ZU, C.I.

KEYWORDS. Cystiscidae, *Cystiscus*, Tuamotu Archipelago, new species.

ABSTRACT. Three new species of *Cystiscus* (Stimpson, 1865) are described from upper reef substrates of the Tuamotu's. These are *Cystiscus carinifer* n. sp., *C. mosaica* n. sp. and *C. nebulosa* n. sp., and their study is based upon the material and data accumulated during two private expeditions to the region undertaken by the second author in 2001 and 2003. Information on the variability of the animal and radula of each species within their respective populations, and discussion of microhabitats and other field observations are provided. These are the first records of the group *Crithe/Cystiscus* from this part of French Polynesia, and the likelihood of the existence of more species in the region is considered to be high since it is generally accepted that the diversity of the group is underestimated in most locations.

It is considered that similarities in patterns of animal chromatism, shell morphology, and radular morphometry show potential for enabling similar species within the group *Crithe/Cystiscus* to be associated together into subgroups. However, the overall taxonomic reorganisation and subdivision of the genera *Crithe* and *Cystiscus* at this time is considered to be premature and too problematic given the current poor understanding of the extent of their global diversity and variability.

INTRODUCTION

Two recent (2001 & 2003) private expeditions to French Polynesia by the second author have provided an opportunity for sampling upper reef substrates for micromolluscs, and in particular have enabled detailed study of the members of the cystiscid genus *Cystiscus* (Stimpson, 1865) that are found there. From a total of four new species discovered, this paper focuses upon three closely related species from the Tuamotu Archipelago (the fourth species discovered is a black and yellow banded species which is presently under study by us).

Coovert (1989) reviewed the radula of *Cystiscus capensis* Stimpson, 1865, the South African type species of the genus, along with three others and later (Coovert & Coovert, 1995) also examined radula SEMs of a further eight Australian species including *C. angasi* (Crosse, 1870), the type species of *Euliginella* (Laseron, 1957). Coovert & Coovert came to the conclusion that all of these species are congeneric based on similar radulae and shell features. The shells of the new species described herein do not exhibit the obovate morphology of *C. capensis* having instead a shell morphology more like that of the genus *Crithe* (Gould, 1860) in that the columellar plications are excavated, an associated parietal callus ridge is present and the shell has an overall subtriangular shape. Coovert and Coovert (1995, p. 70) have stated that 'the radulae of *Crithe* are diagnostic'. Since our own radular studies also indicate that the radulae of both *Cystiscus* and *Crithe* appear to be quite distinct from each other, and as our three new species each have a *Cystiscus* type radula, we have taxonomically assigned them to the genus *Cystiscus*.

Whether taxonomic subdivision is appropriate for this shell morph type awaits further research into the total diversity of the group, but what is becoming clear is that the division of the two genera on the basis of shell morphology alone is too simplistic an approach, and it seems more likely that a combination of radular type, shell morphology and animal chromatism will eventually play a role in species group definitions.

Historically the worker most often associated with this region is William H. Pease (1824-1871), who described many shells from the Tuamotu's, but none from the group under discussion. Bavay (1922) became the first and only author of a French Polynesian representative of the family, *Marginella (Volvaria) micros*, with a type locality of the Tuamotu's. Its correct generic assignment is unclear since the type material is not present in the Bavay collection in the MNHN (F. Boyer pers. comm.), and it was not found at the type locality during the two recent explorations by the second author. We provisionally consider this species to be a *Plesiocystiscus* (Coovert & Coovert, 1995) with reference to its original figure and description, and we consider that no further reference to this species is necessary here.

Many new species of *Cystiscus* were recently presented in a wide ranging review of New Caledonian Cystiscidae by Boyer (2003). Two of the species presented by Boyer, namely *C. goubini*

(Bavay, 1922) and *C. pardus* (Boyer, 2003) share similar shell morphology and animal pattern characteristics with two of our new species, *C. mosaica* and *C. nebulosa* , and these are commented upon in the discussion at the end of this paper.
The Hawaiian *Cystiscus huna* (Kay, 1979) also appears to be close to our new species. It is approximately the same size and is morphologically very similar. Coovert (1987) described its columella as having three excavated plications and an associated parietal callus ridge and he also demonstrated the radula as having 10 cusps per plate arranged asymmetrically about a large central cusp. Further anatomical details of the animal of *C. huna* are unreported and therefore it cannot be further compared with the animals of our new species. The new species herein described as having Cystiscid Type 3 animals (after Coovert, 1995) are characterized by an elongate head that has a longitudinal dorsal split with its anterior end bifurcate, and may either represent ventrally fused tentacles with an associated longitudinal dorsomedial channel or a longitudinally split head completely lacking tentacles. The former interpretation is used provisionally in this study, since a determination on this issue will require detailed anatomical study.

Materials and Methods

All live specimens were obtained by breaking apart friable dead coral lumps into a bowl and waiting for the animals to crawl out of the resulting grit and up the side of the bowl. The coral lumps were taken from <1 to 7 metres by wading, snorkelling or scuba diving.
On the first expedition, photographs were taken of the living animals shortly after collection by the second author, using a Kodak DCS 410 digital single lens reflex camera with a 60mm Nikkor 1:2.8 D macro lens, extension tubes and ring flash. On the second expedition in 2003, the live animal images were taken using a Kodak DCS 760 camera, mounted on an Olympus SZX12 stereo microscope over an aquarium measuring 50mm x 75mm and filled to a depth of 10mm, with the same camera mounted on an Olympus CX41 compound microscope with a x100 PlanApo, oil-immersed lens for the radular images. The radulae were extracted from specimens preserved in denaturalised alcohol using KOH solution and were subsequently mounted for scanning electron microscopy and compound light microscopy. The radulae were assessed for number of plates, number of cusps per plate, pitch (distance between successive plates) and the width of the plates.
All shells referred to in the text are live taken adult specimens unless specified otherwise.

Abbreviations

MNHN: Museum national d'Histoire naturelle, Paris, France.
AWC: Andrew Wakefield Collection.
TMC: Tony McCleery Collection.

SYSTEMATICS

Family **CYSTISCIDAE** Stimpson, 1865
Subfamily **CYSTISCINAE** Stimpson, 1865
Genus ***Cystiscus*** Stimpson, 1865
Type species *Cystiscus capensis* Stimpson, 1865 (non *Marginella capensis* Krauss, 1848) = *Marginella cystiscus* Redfield, 1870 (nom. nov.)

Cystiscus carinifer n. sp.
Figs 1-10, 21-24, 36-44

Type material. Tuamotu Archipelago, Tahanea, holotype (1.56 x 1.05 mm) MNHN. (Figs 21-23).
Tuamotu Archipelago, Tahanea, 2 paratypes (1.43 x 1.07 mm (Fig 24), 1.52 x 1.07 mm), MNHN.
Tuamotu Archipelago, Tahanea, 2 paratypes (1.43 x 1.02 mm, 1.49 x 1.01 mm), TMC.
Tuamotu Archipelago, Tahanea, 4 paratypes (1.47 x 1.10 mm, 1.49 x 1.09 mm, 1.58 x 1.12 mm, 1.50 x 1.08 mm), AWC.

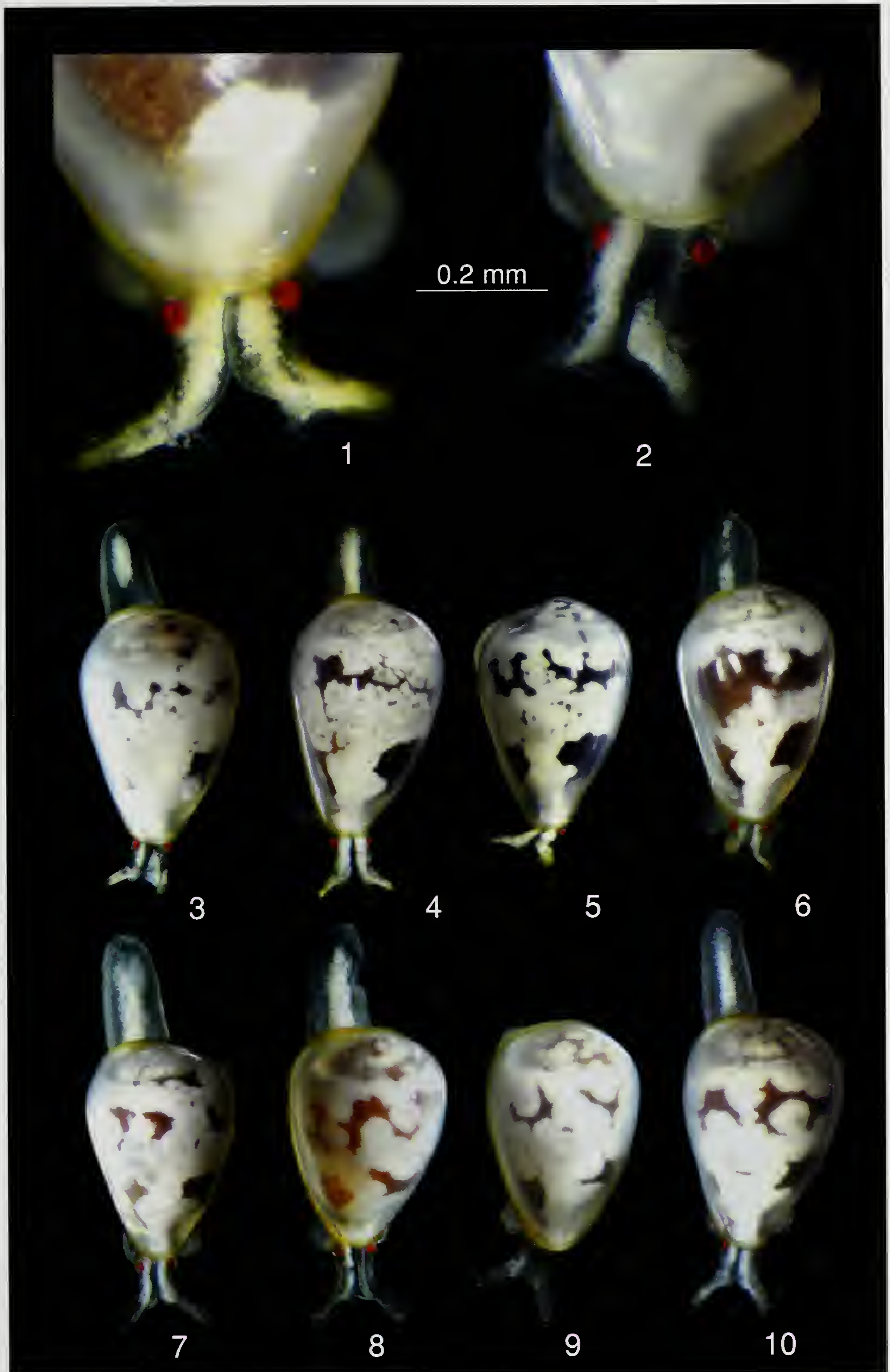
Other material examined. Tuamotu Archipelago, Tahanea, near West Pass, 2 specimens in alcohol, AWC; 43 specimens, TMC; Makemo, 6 specimens, TMC.

Type Locality. Tahanea, Tuamotu archipelago.

Distribution. Tahanea, and Makemo Atolls, Tuamotu Archipelago.

Habitat. From <1 to 7 metres in the interstices of dead coral lumps, from pass reef areas.

Figures 1-10 *Cystiscus carinifer* n.sp.
1-2. Detail of head anatomy of 2 specimens from Tahanea.
3-6. Tahanea, Tuamotu's, 3-7 m in dead coral, 4 specimens, length 1.43-1.52 mm.
7-10.Makemo, Tuamotu's, 1-2 metres in dead coral, 4 specimens, length 1.43-1.50 mm.


0.2 mm
1
2
3
4
5
6
7
8
9
10

Description. Shell small, of two whorls (including nucleus), transparent, smooth, glossy, triangular, moderately rounded shoulder, spire low, apical callus absent. Aperture fairly parallel for posterior half then widening anteriorly. Lip smooth, thickened posteriorly, with a thin external varix or beading in mature specimens. Posterior edge of lip sweeps anteriorly then back posteriorly to insert at level of suture. Distinct bulge in posterior half of last adult whorl just before lip recurvature. Marked parietal callus extending full length of aperture, including plications. Four strong columellar plications, occupying just less than 50% of apertural length.

First plication strongly emergent, joining up externally with anterior end of labial varix. Plications excavated inside aperture. Plications square in cross section, becoming more rounded after the excavated area as they enter within aperture. Columella weakly lirate in some specimens. Thin callus wash from second columellar plication passing round body whorl to anterior extremity.

Paratypes and other material examined similar in all respects to holotype. Adult shell size range min. 1.4 x 1.0mm, max. 1.6 x 1.15 mm (holotype 1.56 x 1.05 mm).

Animal: based on a study of several animals from Tahanea and Makemo, Type 3 animal (Figs 1-10). Tentacles short, fine, situated at anterior position on head. Head split longitudinally along superior aspect. Lower anterior border ciliated. Eyes small, red, set well back from tentacles within lateral bulges on head. Foot half width of shell. Propodium widened anteriorly. Head with a pair of opaque white lines, medial to eyes, one extending into each tentacle its full length. Internal mantle dark reddish brown superimposed with large creamy white blotches roughly concentrated into spiral zones at the shoulder and midbody, with a dorsal extension from the latter in an anterior direction. Creamy white markings in Makemo population appear more circular and distinct than those of the Tahanea population but the organisation of the pattern remains constant. Spire also mottled cream and reddish brown. External mantle translucent with yellow tint. Foot translucent except for fringe of opaque white, and an opaque white zone occupying its central third, running longitudinally down the midline.

Radula: SEM examination of a radula from an adult specimen from the type locality (Figs 36-38); cystiscid type 2 radula, 260 'V' shaped rachidian plates, 9µm in width, variable cusp count per plate of 7-9 cusps, most plates bearing a central cusp with 3 lateral cusps on either side. Occasional plates bearing a very small extra cusp between the central cusp and first lateral, on one or both sides of the central cusp (Figs 41, 42).

An examination of eight radulae from specimens from Tahanea and Makemo was performed with the compound microscope. The results are summarised in table 1. These show a cystiscid type 2 radula, 225-262 plates, each bearing 7 cusps. The pitch of the plates varied from 2.43 to 2.86 µm and the ribbon was 7.6 to 10 µm in width. An example of one of these is shown in Figs 43, 44.

Shell length (mm)	No. of plates	No. of cusps	Pitch (µ)	Width (µ)	W:P index
1.46	248	7	2.95	9.26	3.14
1.47	250	7	2.86	10.0	3.50
1.50	225	7	2.85	9.10	3.19
1.50	229	7	2.76	9.20	3.33
1.39	250	7	2.68	8.70	3.25
1.55	262	7	2.52	9.00	3.57
1.45	260	7	2.50	7.60	3.04
1.41	250	7	2.43	9.00	3.70

Table 1. Radular analysis of *Cystiscus carinifer* n. sp.

Remarks. The living animals of this species were observed under high power light microscopy and it was observed that cilia were present on the leading edge of the lower border of the head/siphon complex (Fig 1), but cease at a point approximately half way along the tentacles. It is possible that the whole of the 'tube' which forms the head is lined with ciliated epithelium. Histological studies will be required to establish the form and true functional significance of this anatomical feature, which has also been observed on other as yet undescribed species of South Pacific *Cystiscus*.
This species was generally found in deeper water than the other two, with most of the dead coral lumps containing specimens coming from 3 to 7 metres. It was observed that the coral lumps in Tahanea have much green weed coverage, whereas this is not present on the silted up coral from other atolls. The ideal microhabitat for *C. carinifer* is therefore the interstices of weed covered dead coral pieces, although the species does seem to be able to adapt to less than ideal circumstances, as evidenced by its presence on Makemo.
In contrast with most other recorded Indo-Pacific *Cystiscus* species which have either a banded or a diffusely reticulated pattern of the internal mantle, *C. carinifer* has large, bold and variable markings.
These markings tend to be concentrated at midbody and shoulder zones, which is a pattern observed in some banded *Cystiscus*. Thus the pattern of *C. carinifer* could be interpreted as either a banded species with a very disrupted banded pattern, or an intermediate form between distinctly banded and evenly mottled or mosaic-like pattern schemes. Further analysis of pattern schemes and their variability (both within and between species) of many species of *Cystiscus* will be required before meaningful conclusions can be reached.

Etymology. *Cystiscus carinifer* is named for the lateral profile of the strongly emergent first columellar plication (Fig 23), from the Latin *carina* (f.): keel of a ship.

Cystiscus mosaica n. sp.
Figs 11-15, 25-28, 45-47

Type Material. Tuamotu Archipelago, Makemo, holotype (1.51 x 1.07 mm) MNHN (Figs 25-27).
Tuamotu Archipelago, Makemo, paratype (1.43 x 1.01 mm) MNHN (Fig 28).
Tuamotu Archipelago, Makemo, paratypes, 2 specimens (1.47 x 1.05 mm, 1.45 x 1.04 mm) TMC.
Tuamotu Archipelago, Makemo, paratypes, 2 specimens (1.46 x 1.04 mm, 1.55 x 1.10 mm) AWC.

Other material examined. 1 adult & 9 juvenile specimens, plus 2 dead adult shells, Makemo. TMC.

Type Locality. Makemo Atoll, Tuamotu Archipelago.

Distribution. Currently known only from the type locality.

Habitat. Lives within interstices of dead coral lumps in shallow water (<1-3m) in and around passes in the reef.

Description. Shell small, of two whorls (including nucleus), transparent, smooth, glossy, triangular, moderately rounded shoulder, spire low, apical callus absent. Aperture fairly parallel for posterior half then widening anteriorly. Lip smooth, thickened posteriorly, with a thin external varix or beading in mature specimens. Posterior edge of lip sweeps anteriorly then back posteriorly to insert at level of suture, forming a rostration in very mature specimens. Distinct bulge in posterior half of last adult whorl just before lip recurves. Substantial parietal callus extending full length of aperture, including plications, thick enough to render shell opaque. Four strong columellar plications, occupying just less than 50% of apertural length. First plication strongly emergent, joining up externally with anterior end of labial varix. Plications excavated inside aperture. Plications square in cross section, becoming more rounded after the excavated area as they enter within aperture. Columella weakly lirate in some specimens. Callus wash from second columellar plication passing round last adult whorl to anterior extremity.
Paratypes and other material examined similar in all respects to holotype. Adult shell size (L) range min. 1.46 mm, max., 1.51 mm (holotype 1.51 x 1.07 mm).
Animal: based on a study of several animals from Makemo, Type 3 animal (Figs 11-15). Tentacles short, fine, situated at anterior position on head. Head split longitudinally along superior aspect. Eyes small, red, set well back from tentacles within lateral bulges on head. Foot half width of shell. Propodium widened anteriorly. Head with a pair of weakly opaque cream lines, medial to eyes, not extending into tentacles. Internal mantle evenly very pale mauve superimposed with pale cream reticulation resulting in a mosaic-like pattern. External mantle translucent yellowish-cream. Foot translucent with very weak opaque cream zone occupying its central third, running longitudinally down the midline. An examination of two radulae from specimens from Makemo was performed with the compound microscope. The results are summarised in table 2. These reveal a cystiscid type 2 radula, of 230 to 276 plates, each plate bearing 8 cusps (occurring due to an extra cusp adjacent to the large central cusp). The width of the ribbon is 12.4-13.4 μm. An example of one of these radulae is shown in figs 45-47.

Shell length (mm)	No. of plates	No. of cusps	Pitch (μ)	Width (μ)	W:P index
1.56	230	8	3.43	13.4	3.9
1.51	276	8	2.95	12.4	4.2

Table 2. Radular analysis of *Cystiscus mosaica* n. sp.

Remarks. Although the similarities in shell morphology between all three of the species described here is profound, it is possible when studying them in large enough numbers to perceive small differences which help in their differentiation. In the majority of specimens *C. mosaica* has a substantial parietal callus wash, and a much greater tendency to extend this callus to the labial shoulder creating a noticeable 'rostration', particularly in older specimens. The callus deposits of *C. carinifer* and *C. nebulosa* are consistently less than those of *C. mosaica*.

Comparisons between *C. mosaica* and the other two species can also be made from observations of radular characters. The features found to be of importance were the cusp count and the radular widths. The cusp count of *C. mosaica* is higher at mainly 8 per plate compared to mainly 7 for *C. carinifer* and *C. nebulosa*, and comes about by an extra cusp regularly appearing adjacent to the large central cusp. This extra cusp in *C. mosaica* seems to relate to the greater width of the plate (approx 25% wider than the other two species) and can therefore be considered to be a constant specific character. The presence of an extra cusp was also observed in the SEM examination of *C. carinifer* but occurred to a much lesser extent than in *C. mosaica*. The measurement of the relative widths of the radulae revealed that (in the limited number of specimens examined) the plate width of *C. mosaica* was consistently 2-3μm wider than that of *C. nebulosa*, and consistently 3-4μm wider than that of *C. carinifer*. No individual *C. nebulosa* radula was greater than 10.45 μm in width and no individual *C. mosaica* radula was less than 12.4mm in width, representing a significant 20% difference. The study of radular characters in species differentiation in the group *Crithe/Cystiscus* is still in its infancy and as a result these observations need to be interpreted with caution, and not in isolation from other characters of the animal and shell.

From the point of view of animal chromatism, *C. mosaica* appears to be closer to *C. nebulosa* than to *C. carinifer*. It differs from the former in having a more well defined pattern, being overall creamy insead of yellow, and in lacking the strong midline opacity of the foot and tentacles.

Etymology. Named after the 'mosaic-like' pattern of the internal mantle. From French 'mosaique', based on Latin *musi(v)um* ('decoration with small square stones'). Modern Latin *mosaicus* of late middle English origin ('pattern produced by arranging together small pieces of material').

Cystiscus nebulosa n. sp.
Figs 16-20, 29-35, 48, 49

Type Material. Tuamotu Archipelago, Faaite, holotype (1.40 X 0.99 mm) MNHN (Figs 29-31).
Tuamotu Archipelago, Faaite, paratype (1.58 x 1.04 mm) MNHN (Fig 32).
Tuamotu Archipelago, Faaite, paratypes, 3 specimens (1.43 x 1.06 mm, 1.43 x 1.04 mm, 1.50 x 1.07 mm), AWC.
Tuamotu Archipelago, Faaite, paratypes, 2 specimens (1.45 x 1.05 mm, 1.45 x 1.04 mm), TMC.

Other material examined. Faaite, 35 specimens, TMC.

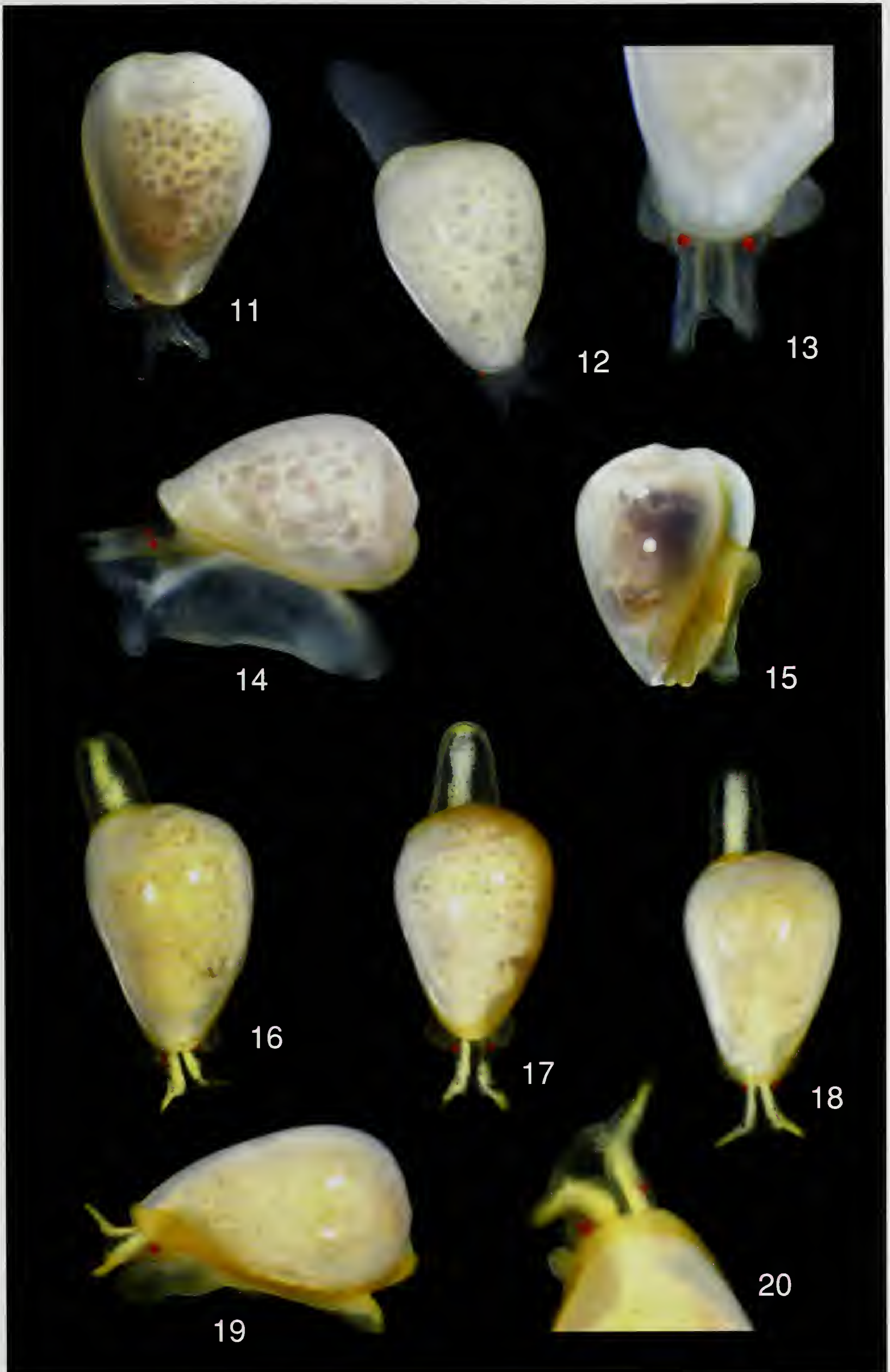
Type Locality. Faaite Atoll, Tuamotu Archipelago.

Distribution. Currently known only from type locality.

Habitat. Lives within interstices of dead coral lumps in shallow water (<1-3 m) in and around passes in the reef.

Figures 11-20

11-15. *Cystiscus mosaica* n.sp., Makemo, Tuamotu's. 11. length 1.50 mm; 12-15. length 1.51 mm.
Figs. 16-20 *Cystiscus nebulosa* n.sp., Faaite, Tuamotu's. 16. length 1.45 mm; 17. length 1.47 mm; 18-20. length 1.51 mm.


11
12
13
14
15
16
17
18
19
20

Description Shell small, of two whorls (including nucleus), transparent, smooth, glossy, triangular, moderately rounded shoulder, spire low, apical callus absent. Aperture fairly parallel for posterior half then widening anteriorly. Lip smooth, thickened posteriorly, with a thin external varix or beading in mature specimens. Posterior edge of lip sweeps anteriorly then back posteriorly to insert at level of suture. Distinct bulge in posterior half of last adult whorl just before lip recurvature. Marked parietal callus extending full length of aperture, including plications. Four strong columellar plications, occupying just less than 50% of apertural length. First plication strongly emergent, joining up externally with anterior end of labial varix. Plications excavated inside aperture. Plications square in cross section, becoming more rounded after the excavated area as they enter within aperture. Columella weakly lirate in some specimens. Thin callus wash from second columellar plication passing round last adult whorl to anterior extremity.

Paratypes and other material examined similar in all respects to holotype. Adult shell size range min. 1.38 x 0.99 mm, max. 1.58 x 1.04 mm (holotype 1.43 x 1.06 mm).

Animal: based on a study of several animals from Faaite Atoll, Type 3 animal (Figs 16-20). Tentacles short, fine, situated at anterior position on head. Head split longitudinally along superior aspect. Eyes small, red, set well back from tentacles within lateral bulges on head. Foot half width of shell. Propodium widened anteriorly. Head with a pair of opaque creamy-yellow lines, medial to eyes, each extending into its respective tentacle. Internal mantle creamy-yellow with wisps of darker cream forming nebulous pattern over the whole of the internal mantle. External mantle lemon yellow. Foot translucent with a wide opaque creamy-yellow zone occupying its central third, running longitudinally down the midline.

Shell length (mm)	No. of plates	No. of cusps	Pitch (μ)	Width (μ)	W:P index
1.54	223	7	3.10	10.45	3.37
1.46	245	7	2.96	10.0	3.40
1.46	223	7	2.74	10.1	3.70

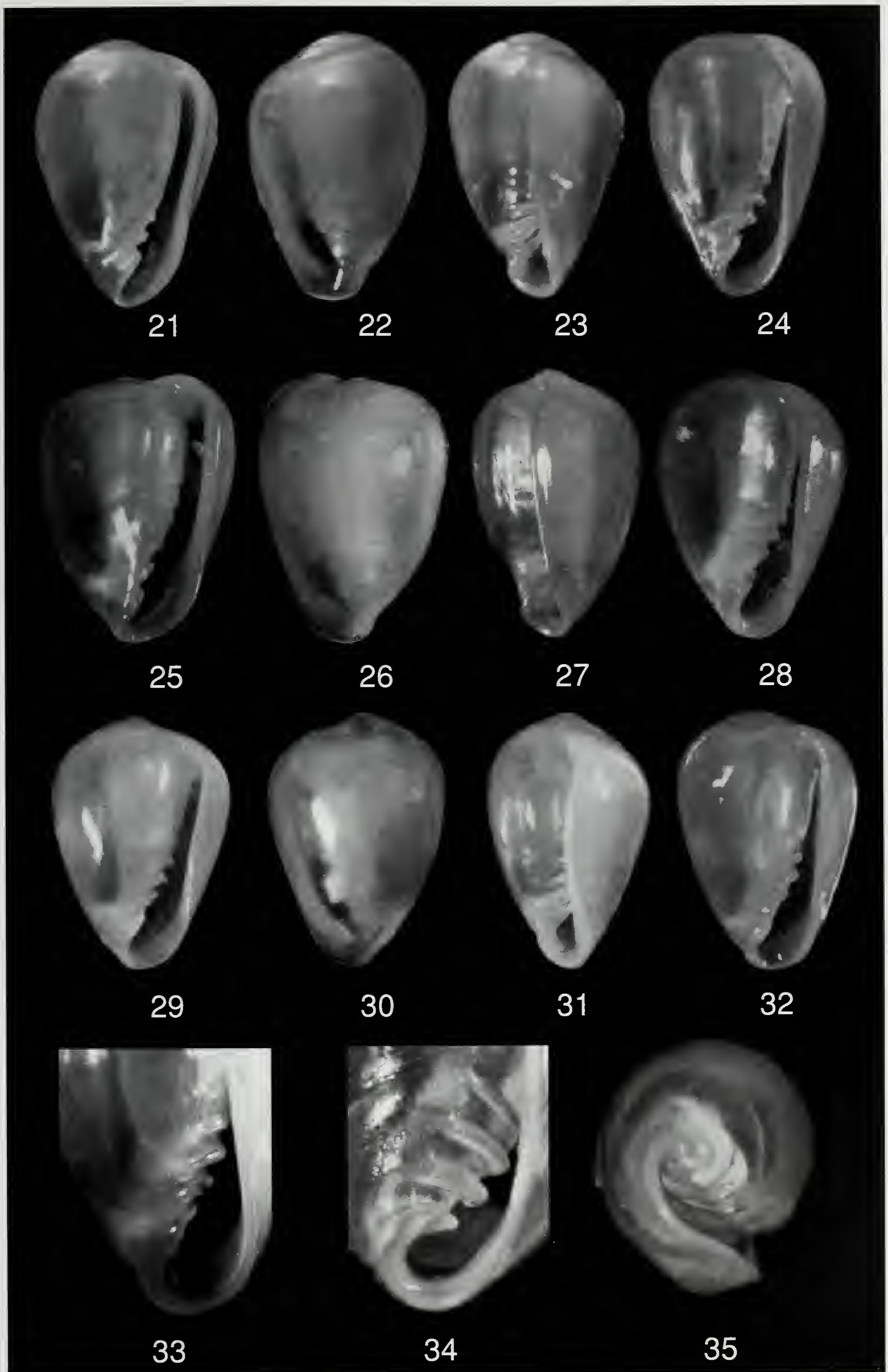
Table 3. Radular analysis of *Cystiscus nebulosa* n. sp.

An examination of three radulae from specimens from Faaite was performed under the compound microscope. The results are summarised in table 3. These reveal a cystiscid type 2 radula, of 223-245 v-shaped overlapping plates, each plate approximately 10 μm wide and bearing 7 cusps. Examples of two of these radulae are shown in figs 48 and 49.

Remarks. When attempting to make comparisons and establish links between different species of *Cystiscus* whose shells are extremely similar, a close examination of the chromatism of the animals is the most important way of determining their relationships. We have observed that the 'billowing cloud-like' pattern of the internal mantle of *C. nebulosa* is also present in the white zones on the mantle of many specimens of *C. carinifer* from Tahanea (see Fig 4). In addition *C. nebulosa* and *C. carinifer,* both bear strong opacities in the midline of the foot, and head and tentacle regions. We have noted however that within populations of both species that there is some variability in the development of these opacities, in that the head markings in occasional specimens exhibit unilateral incomplete development (Figs 2, 17). The foot markings are also variable in their presentation (Figs 3, 4, 6, 10, 17, 18). Based upon these features, we conclude that there is a close relationship between *C. carinifer* and *C. nebulosa*. The different structure of the reticulated pattern on the mantle of *C. mosaica*, and the absence of body opacities leads us to the conclusion that *C. mosaica* is not as closely related to the other two as they are to each other.

Figures 21-35

Figs. 21-24 *C. carinifer* n.sp., Tahanea, Tuamotu's, 7 metres in dead coral.
21-23. Holotype (1.56 x 1.05 mm) MNHN; 24. Paratype 1 (1.43 x 1.07 mm) MNHN.
Figs. 25-28 *C. mosaica* n.sp., Makemo, Tuamotu's, 2 metres in dead coral.
25-27. Holotype (1.51 x 1.05 mm) MNHN; 28. Paratype 1 (1.43 x 1.01 mm) MNHN.
Figs. 29-35 *C. nebulosa* n.sp., Faaite, Tuamotu's, 3 metres in dead coral.
29-31. Holotype (1.40 x 0.99 mm) MNHN; 32. Paratype 1 (1.58 x1.04 mm) MNHN; 33-34. Detail of plications; 35. View from below illustrating labial bulge in a mature adult specimen.


21
22
23
24
25
26
27
28
29
30
31
32
33
34
35

Etymology. Named after the 'cloud-like' pattern of the internal mantle. Latin *nebulosus* from *nebula* ('mist'). Origin late middle English (in the sense 'cloudy').

DISCUSSION

The Cystiscidae of shallow reef formations of New Caledonia were recently reviewed by Boyer (2003) in a paper covering the genera *Gibberula*, *Crithe*, *Plesiocystiscus* and *Cystiscus*. Previously named species were reviewed and many new species were described, including thirteen new species of *Cystiscus*. Two of these, *C. goubini* (Bavay, 1922) and *C. pardus* (Boyer, 2003), could be considered analogous with *C. mosaica* n.sp. and *C. nebulosa* n.sp. respectively, in that they share similar pattern design of their internal mantles. An objective comparison of the animal is difficult to achieve when comparing drawings with photographs, but the internal mantle of *C. mosaica* does appear to have a similar mosaic-like reticulated pattern to that of the 'paving pattern' [sic.] of *C. goubini* as shown in the drawings and description of the live animal in Boyer (2003). However, the base colour of the internal mantle is not the same in these two species, being a pale cream in *C. mosaica* and greyish blue in *C. goubini*. An additional difference is that the average shell length of *C. goubini* (1.9 to 2.3 mm) is considerably greater than that of *C. mosaica* (1.46 to 1.51 mm), with no overlap. The relationship between *C. nebulosa* and *C. pardus* seems closer. The internal mantle pattern, presence of white opacity in the foot, shell size and morphology are shared characters. Again, the colouration of the mottled areas in the internal mantle differ, with *C. pardus* being greyish blue on a yellowish background, compared to yellow on a paler yellow background in *C. nebulosa*.

Unlike the two New Caledonian species, *C. mosaica* and *C. nebulosa* were not found in micro-sympatry.

During the course of our fieldwork and subsequent study of the material obtained, it has been possible to make some observations on shallow water representatives of the genus *Cystiscus* in the South Pacific.

The method of collection employed by the authors precluded most behavioural observations of individual animals in their natural habitat. However, the second author repeatedly observed that a return visit to a previously cystiscid rich site the day following initial sampling often yielded a disappointingly low number of specimens, or none at all. A probable explanation for this is that colonies of *Cystiscus* are often small or very compact and they were therefore easily missed on the second occasion.

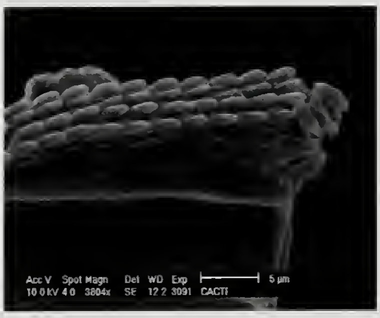
For example during the first expedition to Faaite in the Tuamotu's, 8 adult specimens of *C. nebulosa* were all collected during one snorkelling session only. Four further efforts were made in the 100 metres (approx.) of reef edge there present, specifically in the hope of finding more of this particular species, but none were found until a second search was performed there two years later. From this it can be deduced that in silty, perhaps less than ideal habitats they form compact colonies of animals restricted to a single coral lump rather than being evenly and thinly distributed across the reef, and that neighbouring colonies are indeed present but are few and far between with only occasional coral lumps being colonised.

At other localities, presumably where conditions are more favourable, large populations can be encountered. For example, specimens of *C. carinifer* from Tahanea were found with regularity on repeated dives involving two reefs and covering a large area. The reef systems and water clarity in Tahanea are particularly pristine, and it seems that such conditions favour the establishment of large widespread populations instead of smaller and more isolated ones.

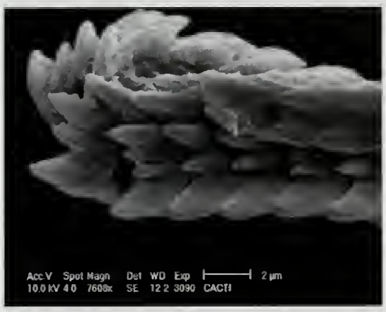
The small population of *C. carinifer* encountered on Makemo is possibly derived from a dispersal from the main population in Tahanea. The Makemo habitat is not as ideal as that found in Tahanea which suggests that in this species at least there is some capacity for dispersal and an ability for a sustainable population to adapt to a slightly different habitat. If such dispersal events and adaptations were to be commonplace in this group *Crithe/Cystiscus*, it would provide an explanation for its great diversity.

Figures 36-49

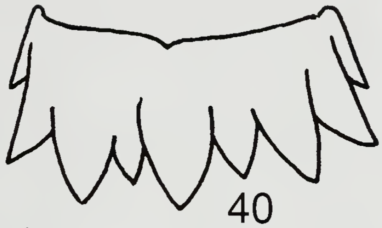
Figs 36-44 Radula of *C. carinifer*, Tahanea.
36-38. Scanning electron microscope views of radula; 39. Diagrammatic representation of lateral view of a single plate; 40-42. Diagrammatic representation of plate variability due to unilateral and bilateral division of lateral cusp; 43-44. Compound microscope view of radula (from shell 1.39 x 1.01 mm). Mag. x2750.
Figs 45-47 Radula of *C. mosaica*, Makemo. (from shell 1.56 x 1.01 mm). Mag. x1400.
45. Focused on cusps; 46. Focused mid-way through plates; 47. Focused on back of plates.
Figs 48-49 Radula of *C. nebulosa*, Faaite.
48. From shell 1.54 x 1.04. Mag. x1250; 49. From shell 1.46 x 1.05. Mag. x2700.

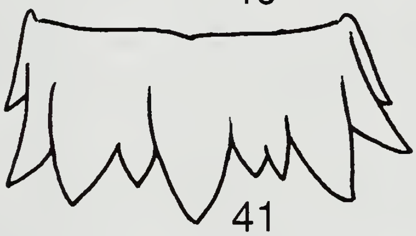

36

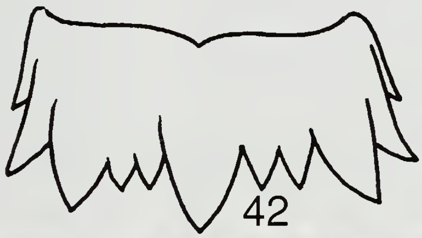

37

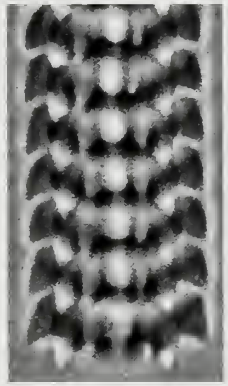

38


39

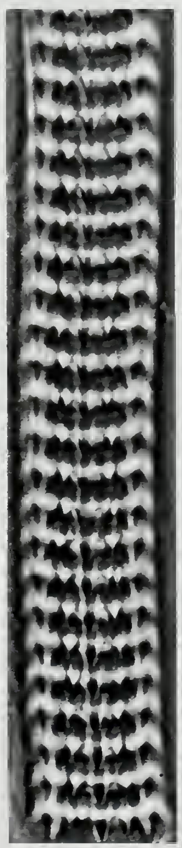

40

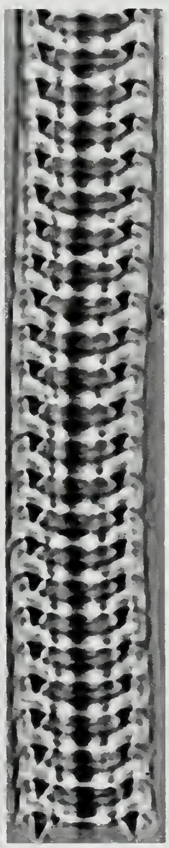

41

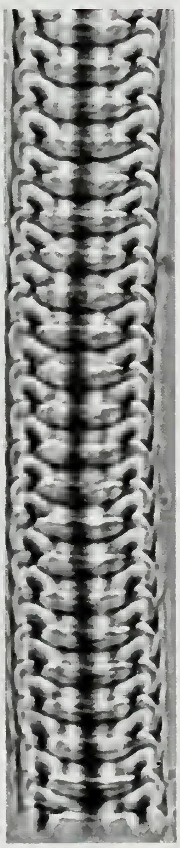

42


43


44


45


46


47


48


49

The second author has observed that irrespective of season, there are always a high proportion of gravid females within *Cystiscus* populations. Murray (1970) observed that in the case of *C. minutissimus* (Tenison-Woods, 1876) well developed juveniles hatched from egg capsules deposited on the bryozoan *Amathia biseriata* (Krauss, 1837), after a 6-7 week gestation period. It is likely therefore that these animals develop and reach maturity very quickly. Such high reproductive capacity in combination with occasional dispersal events would lead to the establishment of isolated populations which could, given sufficient time, become new species in their own right.

We have also observed that when there are only several specimens present in a large bowl of grit, the animals are able to locate each other and group together very rapidly. The mechanism by which they accomplish this is unknown. If this location mechanism is used under normal conditions out on the reef this would explain the ready formation of compact colonies in this group. The second author has experienced other genera (particularly *Plesiocystiscus*) exuding a slimy mucus when handled, so it is possible that chemical defensive and communication mechanisms are well used by these groups, and that these apparently simple animals are more complex than first thought.

The shell morphologies of each of these three new species are very similar and it would be very difficult to attempt an identification on the basis of the shell alone. The decision whether to confer specific status has been made armed with an understanding of the degree of variability of the colour and pattern of the animals. Both authors have observed living *Cystiscus* populations in the Indian and Pacific Oceans and have discovered that the shells of many species appear very similar and can be difficult to separate morphologically. Therefore, in most cases the information provided by accurate locality data and detailed animal observation in tandem with a description of the associated shell is considered vital for the correct allocation of a species from the group *Crithe/Cystiscus* to an existing taxon, or in facilitating its description as a new species.

Acknowledgements

The authors are indebted to Emilio Rolan for radular extractions, SEM photography and valuable advice.

REFERENCES

Bavay, A. 1922. Coquilles Des Sables Littoraux Marins. Part 2. Deux Marginelles Nouvelles De L'Indo-Pacifique. *Journal de Conchyliologie*, LXVII: 63-64.

Boyer, F. 2003. The Cystiscidae (Caenogastropoda) from upper reef formations of New Caledonia. *Iberus*, 21 (1): 241-272.

Coovert, G. A. 1987. Thoughts on Marginellidae of Hawaii. *Hawaiian Shell News*, 35 (2): 3.

Coovert, G. A. 1989. A literature review and summary of published marginellid radulae. Marginella Marginalia 7 (1-6): 1-37.

Coovert, G.A. and Coovert, H.K. 1995. Revision of the Supraspecific Classification of Marginelliform Gastropods. *The Nautilus* 109 (2-3): 43-110.

Laseron, C.F. 1957. A New Classification of the Australian Marginellidae (Mollusca), with a review of species from the Solanderian and Dampierian Zoogeographical Provinces. *Australian Journal of Marine and Freshwater Research*. 8:274-311.

Murray, F.V. 1970. The reproduction and life history of Microginella minutissima (Tenison-Woods, 1876) (Gastropoda: Marginellidae). *Memoirs of the National Museum of Victoria*. 31:31-35.

Stimpson, W. 1865. On certain genera and families of zoophagous gasteropods. *American Journal of Conchology* 1(1):55-56.